New pygmy grasshoppers in Miocene amber from the Dominican Republic (Orthoptera: Tetrigidae)

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Abstract: Two new pygmy grasshoppers (Orthoptera: Tetrigidae: Cladonotinae) are described from specimens preserved in Early Miocene (Burdigalian) amber from the Dominican Republic. *Antillotettix electrum* sp.nov. and *Baeotettix lottiae* gen. et sp.nov. are the first tetrigids to be described from Dominican amber. An updated list of tetrigid species known from the West Indies is provided.

Key words: Cladonotinae, grouse locusts, ground hoppers, Burdigalian, Hispaniola.

Santrauka: Straipsnyje aprašomos dvi naujos smulkių tiesiasparnių (Orthoptera: Tetrigidae: Cladonotidae) rūšys, išlikusios ankstyvojo mioceno (Burdigalis) gintare iš Dominikos Respublikos. *Antillotettix electrum* sp.nov. ir *Baeotettix lottiae* gen. et sp.nov. yra pirmieji šeimos Tetrigidae vabzdžiai, rasti Dominikos gintare. Pateikiamas atnaujintas Vakarų Indijos šeimos Tetrigidae rūšių sąrašas.

Raktiniai žodžiai: Cladonotinae, Burdigalis, Haitis.

Introduction

Tetrigidae (pygmy grasshoppers, grouse-locusts or ground-hoppers) are a moderately diverse group of basal Caelifera comprising approximately 1400 species in around 270 genera. Readily identified by their elongate pronotum, two-segmented pro- and mesotarsi, and the absence of the arolium between the tarsal claws, tetrigids have an almost cosmopolitan distribution with their greatest diversity encountered in the tropics (Steinmann 1962, 1969, 1970, 1971). They are generally small (less than 15 mm), cryptic insects that usually occur in moist habitats where they feed mostly on algae and bryophytes. Perhaps one of the most intriguing aspects of tetrigid biology is their ability to swim. Riparian species are often capable of swimming well on the surface of water, whilst other more fully aquatic forms are efficient swimmers both above and beneath the surface (Lucas 1920; Amédégnato & Devriese 2008)

The Neotropical Tetrigidae were most recently catalogued by Steinmann (1969) who listed 188 species in 45 genera, though reported only 11 species in five genera from the West Indies. Subsequently, Pérez-Gelabert et al. (1998), Pérez-Gelabert & Otte (1999) and Pérez-Gelabert (2003) described several new genera and more than doubled the number of species known from the West Indies. The tetrigid fauna of North America and Mexico comprises only the subfamilies Batrachideinae and Tetriginae, though in Central and South America the subfamilies Cladonotinae, Lophotettiginae and Metrodorinae are also present (Steinmann 1969, 1971; Pérez-Gelabert et al. 1998). Interestingly, although the Cladonotinae are one of the least dominant subfamilies of New World Tetrigidae, they account for more than 75% of the total numer of tetrigid species known from the West Indies (Table 1). Pérez-Gelabert et al. (1998) suggested that the complex geological and ecological evolution of the region may have fuelled their diversification. Indeed, the ecological complexity of the islands coupled with their dynamic geological history could easily have caused frequent vicariance events promoting allopatric speciation. Any such events would have had profound effects on apterous forms such as the cladonotines due to their limited dispersal abilities.

The Early Miocene (Burdigalian) amber of the Dominican Republic is remarkable for the diversity and exceptional preservation of its biological inclusions (Grimaldi 1996; Grimaldi & Engel 2005). However, work on Dominican amber Orthoptera has lagged behind studies on other insect groups, partly as a result of the rarity of orthopteran inclusions. Six new species of Trigonidiinae (Gryllidae) and the mogoplistid *Ornebius ambericus* were described by Vickery & Poinar (1994) and a eumastacid grasshopper, *Paleomastacris amberinus* was described by Pérez-Gelabert et al. (1997). Aside from these two studies however, little has been pub-

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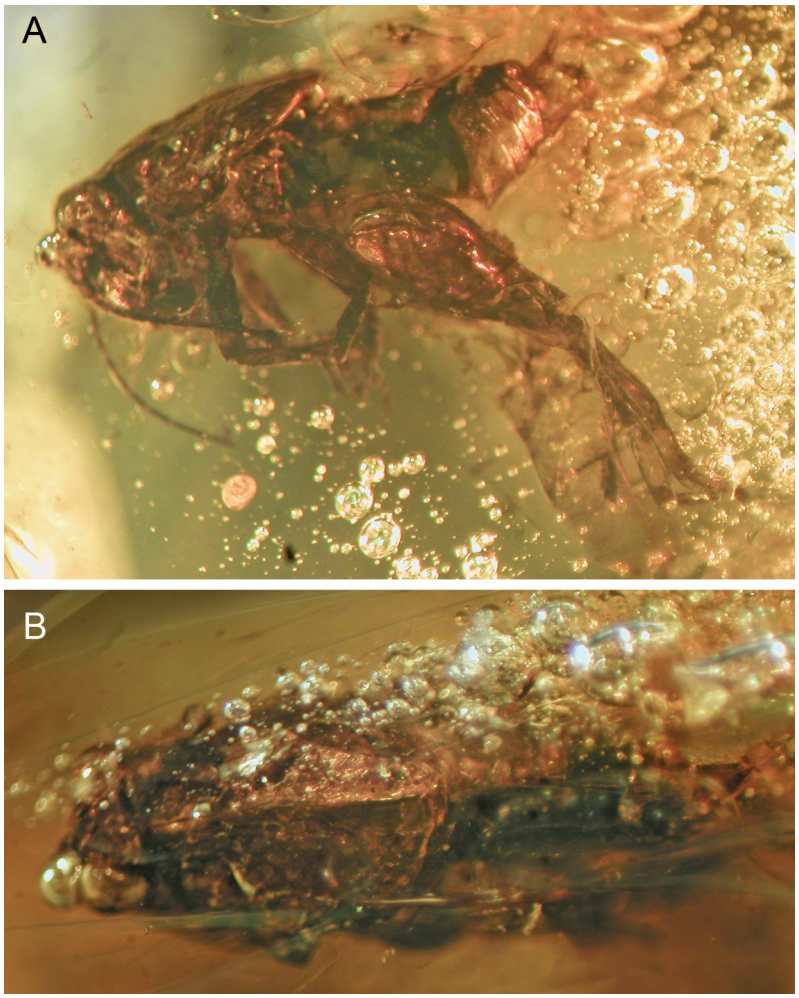


Fig. 1: Holotype of *Antillotettix electrum* sp.nov. (AMNH DR-14-1152); (**A**) lateral view of habitus; and (**B**) dorsal view of pronotum. Dimensions are given in the text.

lished on Dominican amber Orthoptera. Trigonidiine gryllids dominate the orthopteran assemblage and are fairly common, though numerous other taxa are also present including Gryllotalpidae, Tettigoniidae, Tetrigidae and Tridactylidae. Here, I describe the first pygmy grasshoppers from Dominican amber and provide an updated list of Tetrigidae from the West Indies (Table 1).

The specimens described here are deposited in the amber collection of the Division of Invertebrate Zoology (Entomology), American Museum of Natural History, New York (AMNH). Terminology generally follows UVAROV (1966). The age and origin of Dominican amber is reviewed by ITTURALDE-VINENT & MACPHEE (1996), GRIMALDI & ENGEL (2005) and PENNEY (2008).

Systematic account

Family Tetrigidae AUDINET-SERVILLE, 1838

Subfamily Cladonotinae BOLIVAR, 1887

Cladonotae BOLIVAR, 1887: Annales de la Société Entomologique de Belgique **31**, 175.
Cladonotinae REHN, 1952: Grasshoppers and locusts (Acridoidea) of Australia **1**, 24.

Type genus: *Cladonotus* SAUSSURE, 1862.

Remarks: Cladonotinae are entirely apterous and readily distinguished from the other tetrigid subfamilies by the widely forked frontal costa and markedly elevated pronotum. Cladonotines are highly cryptic tetrigids and the pronotum often bears a striking leaf-like projection or is ornately sculpted in order to blend in amongst the leaf litter. The subfamily as currently defined comprises around 46 genera and has a circumtropical distribution.

Genus *Antillotettix* PÉREZ-GELABERT, 2003

Antillotettix PÉREZ-GELABERT, 2003: Journal of Orthoptera Research **12**, 111.

Type species: *Antillotettix nanus* PÉREZ-GELABERT, 2003 by original designation.

Diagnosis: This genus can be distinguished from other Neotropical Cladonotinae by its very small size (4-7 mm) and distinctive pronotal morphology. The pronotum in *Antillotettix* is only very slightly tectate anteriorly, covering the cervical region but not projecting far over the head itself, and is not markedly pronounced dorsally as in most other cladonotines. *Antillotettix* is morphologically most similar to *Mucrotettix* PÉREZ-GELABERT et al., 1998 and *Truncotettix* PÉREZ-GELABERT et al., 1998, though is easily distinguished from the latter two genera by the acute bifurcation of the frontal costa, which is markedly obtuse in *Mucrotettix* and *Truncotettix*. The posterior margin of the pronotum in *Antillotettix* is somewhat invaginated forming a median notch similar to that seen in *Truncotettix*, though the notch is generally more pronounced in *Antillotettix* (though see PÉREZ-GELABERT 2003 fig. 7).

Antillotettix electrum sp.nov. (Figs 1-3)

Holotype: ♂, Dominican Republic, Hispaniola; Early Miocene (Burdigalian; 18-20 Ma) Dominican amber; specimen number DR-14-1152 (AMNH).

Etymology: The specific epithet is a noun in apposition and is one of the Latin words for amber. The word *electrum* derives from the latinization of the Greek word ηλεκτρον which appears in Homer's "Odyssey" (c. 700 BC) in reference to an alloy of gold and silver. The word was later used to refer to amber, presumably because of its pale golden colour.

Diagnosis: The new species differs from its congener *A. nanus* in possessing longer antennae (almost twice as long as profemur), less granulose integument, a markedly shorter pronotum and a smaller humeral sinus. The holotype of *A. electrum* is also somewhat smaller than *A. nanus*.

Description: ♂, 3.96 mm long measured from head to abdominal apex; body form rounded with granulose integument. **Head**: globose, not covered by pronotum dorsally; vertex with median carina, fastigium not produced anteriorly; frons mostly obscured by bubbles in the amber; suboccular furrow prominent, deep; mouthparts largely obscured by detritus; eyes globose and bulging, almost in contact with the anterior pronotal margin; occiput mostly covered by the anterior pronotal tectum; antennae filiform, twice as long as profemur, composed of 10 articles; scape robust, almost twice as long as pedicel; flagellomeres of almost uniform size, as long as scape, more than twice as long as wide. **Thorax**: pronotum elevated only slightly higher than the head (Fig. 1), with prominent median carina (Fig. 2); lateral carinae indistinct; pronotal lobes subquadrate, with rounded pleural margin; humeral sinus gently rounded (Fig. 3); pronotum only covering less than half of the abdomen; posterior margin with slight medial notch. **Legs**: pro- and mesofemora quadrate in cross-section, not markedly compressed, with longitudinal row of fine denticles on the ventral angles; pro- and mesotibiae subquadrate in cross-section, narrowing distally with irregular rows of very fine denticles dorsally; mesofemur large, robust with prominent superior carina; externomedian area distinct with prominent transverse facets; genicular lobes of metafemora poorly preserved but apparently well-developed and not bearing denticles; metatibia as long as metafemur, with few dorsal spines and at least four strong apical spines arranged in a subcoronate pattern; metabasitarsus with three pairs of pulvilli. **Abdomen**: upturned within the apical third; subgenital plate longer than wide, tapering posteriorly; cerci extending beyond the abdominal apex, slightly longer than subgenital plate and narrowing to a fine point distally.

Remarks: *Antillotettix electrum* agrees in general body form with *A. nanus* but differs significantly in several aspects. The antennae are notably longer in *A. electrum*, being almost twice as long as the profemur. In *A. nanus*, the antennae are only slightly longer than the profemur. The pronotum of *A. electrum* is also unusually short for a cladonotine and only covers the first and second segments of the abdomen. In males of *A. nanus*, the pronotum extends back much further, covering the entire abdomen. The medial notch of the posterior margin in *A. electrum* is shallower than in the majority of *A. nanus* specimens, though PÉREZ-GELABERT (2003, fig. 7) figured a single male from Jánico with a shallow medial notch not dissimilar to that of *A. electrum*, and suggested that it may represent a seperate species. The Jánico specimen is nonetheless distinct from *A. electrum* based on its body size and pronotal length (see PÉREZ-GELABERT 2003, table 1).

Table 1: Updated list of tetrigid species known from the West Indies. Distribution abbreviations follow PÉREZ-GELABERT et al. (1998): BAH, Bahamas; CA, Central America; CU, Cuba; FLA, Florida; GRE, Grenada; HIS, Hispaniola; JAM, Jamaica; MEX, Mexico; NA, North America; PR, Puerto Rico; TRI, Trinidad; SA, South America; SV, St Vincent.

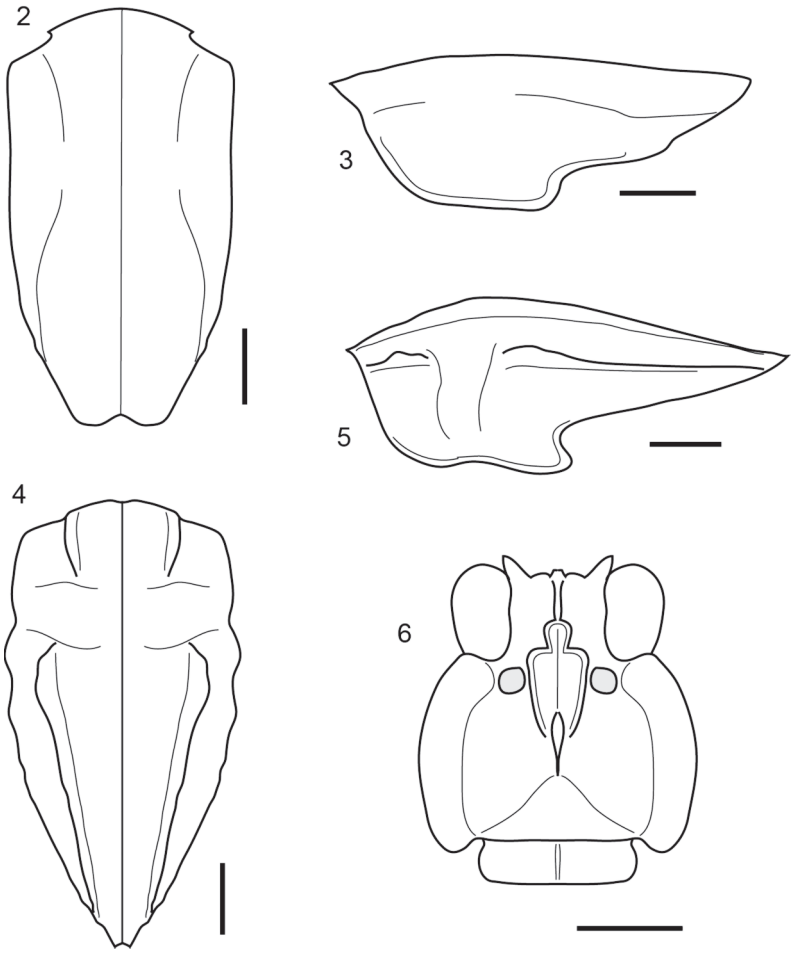
Taxon	Distribution
Subfamily Batrachideinae BOLIVAR, 1887	
Tettigidea empedonepia HUBBELL, 1937	CU, FLA, MEX
Tettigidea lateralis (SAY, 1824)	CU, NA
Tettigidea trinitatis BRUNER, 1906	CU, JAM, CA, SA
Subfamily Cladonotinae BOLIVAR, 1887	
Antillotettix electrum† HEADS, this paper	HIS (Dominican amber)
Antillotettix nanus PEREZ-GELABERT, 2003	HIS
Baeotettix lottiae† HEADS, this paper	HIS (Dominican amber)
Bahorucotettix larimar PEREZ-GELABERT et al., 1998	HIS
Choriphyllum bahamensis PEREZ-GELABERT & OTTE, 1999	BAH
Choriphyllum plagiatum WALKER, 1871	JAM
Choriphyllum sagrai AUDINET-SERVILLE, 1838	CU
Choriphyllum saussurei BOLIVAR, 1887	CU
Cubonotus altinotatus PEREZ-GELABERT et al., 1998	CU
Haitianotettix monstruosus PEREZ-GELABERT et al., 1998	HIS
Haitianotettix tuberculatus PEREZ-GELABERT et al., 1998	HIS
Hottettix haitianus PEREZ-GELABERT et al., 1998	HIS
Mucrotettix gibbosus PEREZ-GELABERT et al., 1998	HIS
Mucrotettix spinifer PEREZ-GELABERT et al., 1998	HIS
Phyllotettix compressus (THUNBERG, 1815)	JAM
Phyllotettix foliatus (HANCOCK, 1902)	JAM
Sierratettix carinatus PEREZ-GELABERT et al., 1998	HIS
Tiburonotus peninsularus PEREZ-GELABERT et al., 1998	HIS
Truncotettix fronterizus PEREZ-GELABERT et al., 1998	HIS
Truncotettix interruptus PEREZ-GELABERT et al., 1998	HIS
Subfamily Tetriginae AUDINET-SERVILLE, 1838	
Micronotus quadriundulatus (REDTENBACHER, 1892)	SV, GRE, HIS, PR, TRI
Paratettix aztecus (SAUSSURE, 1861)	CU, MEX, NA
Paratettix freygessneri BOLIVAR, 1887	CU, HIS, JAM, PR

Genus *Baeotettix* gen.nov.

Type species: *Baeotettix lottiae* sp.nov. by monotypy.

Etymology: The genus-group name is derived from a combination of the Greek prefix "baeo", meaning "small", and the Greek word "tettix", meaning "grasshopper".

Diagnosis: *Baeotettix* can be distinguighed from all other Neotropical Cladonotinae by the morphology of the pronotum and frontal costa. The pronotum bears a prominent medial carina, which although not leaf-like, forms a distinctive crest that is elevated well above the



Figs 2-6: Dominican amber tetrigids. (**2-3**) *Antillotettix electrum* sp.nov., dorsal (**2**) and lateral (**3**) views of pronotum; (**4-6**) *Baeotettix lottiae* gen. et sp.nov., dorsal (**4**) and lateral (**5**) views of pronotum, and anterior view of head capsule (**6**) with mouthparts omitted. Scale bars represent 0.25 mm (**2-3**), 0.5 mm (**4-5**) and 1 mm (**6**).

prozona; the lateral carinae also form prominent ridges which are broken by two shallow transverse sulci (Figs 4-5). The serrate posterior margin of the pronotum is also diagnostic of the genus. The frontal costa is unique amongst Cladonotinae in that the rami are bilobate, with a small proximal lobe and a larger distal lobe forming prominent curved ridges between the antennal fossae (Fig. 6). In all other Neotropical Cladonotinae, the costal rami are unilobate.

Baeotettix lottiae sp.nov. (Figs 4-7)

Holotype: ♂, Dominican Republic, Hispaniola; Early Miocene (Burdigalian; 18-20 Ma) Dominican amber; specimen number DR-15-152 (AMNH).

Etymology: The specific epithet is a noun in the genitive case and is derived from Lottie (a variation of the name Charlotte) after my daughter Charlotte Louise HEADS.

Diagnosis: As for the genus (vide supra).

Description: ♂, 4.85 mm long measured from head to apex of abdomen; body form compact with integument coarsely granular. **Head**: moderately compressed antero-posteriorly, not covered by pronotum dorsally; vertex with strong median carina and two short but prominent fastigial horns; frontal costa forked between the eyes; rami bilobate, converging slightly on each other for a short distance before diverging again, forming two prominent ridges between the antennae; frons covered with tiny tubercles, partly obscured by a bubble in the amber; subocular furrow distinct, taking a broadly curved path from beneath the eye to the anterior tentorial pit; epistomal suture distinct; clypeus broadly rectangular, granular laterally but smooth medially; labrum broad, smooth, markedly larger than clypeus and slightly asymmetrical; mandible strong; maxillary palpi visible just beneath labrum; labial palpi four-segmented, longer and more robust than maxillary palpi; eyes globose and bulging, situated high on the head; antennae filiform, slightly longer than profemur, inserted laterally of the ridges formed by the costal rami; scape robust, slightly longer than the globose pedicel; there are 14 flagellomeres of near uniform width with each flagellomere slightly wider distally; flagellomeres increasing in length distally; penultimate flagellomere markedly shorter than the rest; terminal flagellomere with pointed apex. **Thorax**: pronotum elevated higher than the head in the anterior third, with prominent and well-developed median and lateral carinae; anterior margin of pronotum only slightly tectate, covering the cervical region but not the head; median keel strong, forming a markedly raised, unbroken ridge; lateral carinae prominent, bearing rows of small tubercles, broken by two distinct transverse sulci; integument of pronotum coarsely granular, with several larger and irregularly spaced nodules; pronotum tapering strongly towards posterior, covering almost the entire abdomen; posterior margin serrate, with small yet prominent median notch. **Legs**: profemur subquadrate in cross-section, laterally compressed, with densely granular integument; dorsal surface produced into a broad ridge with a longitudinal row of small denticles; interior ventral margin gently curved; external ventral margin with two denticulate lobes; genicular lobes well-developed and bearing small denticles (see Fig. 7); mesofemur quadrate in cross-section with same granular integument as profemur though not as compressed laterally; dorsal surface expanded; ventral margins denticulate, almost straight; pro- and mesotibiae subquadrate to subcylindrical in cross-section with dorsal row of fine spines and four longer subapical spines on both the interior and exterior ventral margins; metafemur large, robust, with prominent superior carina bearing row of small spines; external medial area with longitudinal median carina bordered by granulose ridges corresponding

to the facets; there is a deep sulcus ventrally in which the metatibia lies; genicular lobes well-developed, broadly rounded, without denticles; metatibia with prominent dorsal margins armed with around 10 spines and numerous small denticles; two small and four large apical spines are arranged in a coronate fashion around the metatibial apex. **Abdomen**: abdominal sternites 1-6 becoming narrower and longer posteriorly; abdominal sternites 7 and 8 much broader; subgenital plate tapering posteriorly, longer than wide, with prominent median sulcus; paraproct slightly longer than subgenital plate; cerci as long as paraproct, surrounded basally by long hairs; epiproct triangular with pointed apex.

Remarks: *Baeotettix* is morphologically similar to *Bahorucotettix* PÉREZ-GELABERT et al., 1998 and *Haitianotettix* PÉREZ-GELABERT et al., 1998. Although almost twice the size of *Baeotettix*, *Bahorucotettix* shares a similarly compact body form and ornamentation of the pro- and mesofemora. *Haitianotettix* is also notably larger than *Baeotettix*, but possesses prominent fastigial horns similar to those of the latter genus. *Bahorucotettix* also has small tuberculate projections of the fastigial area which may be homologous with the horns of *Baeotettix* and *Haitianotettix*. The unusual morphology of the frontal costa and the serrate posterior margin of the pronotum in *Baeotettix* are apparently unique amongst Cladonotinae.

Discussion

Of the 26 tetrigid species recorded from the West Indies, 20 belong to the subfamily Cladonotinae (Table 1). The dominance of Cladonotinae in the West Indies is in stark contrast to the composition of the tetrigid fauna of mainland South and Central America, where Batrachideinae, Lophotettiginae and Tetriginae dominate. The unprecedented diversity of cladonotines in the Caribbean might be explained by the repeated geographical isolation of populations following numerous vicariance events that must have occurred during the complex geological evolution of the region. Indeed, the distributions of modern cladonotine genera on Hispaniola are very restricted (see PÉREZ-GELABERT et al. 1998) and it would appear that members of the subfamily are particularly susceptible to vicariant isolation, due in part no doubt to their aptery, with the inability to fly limiting their dispersal potential.

Cladonotinae are highly cryptic tetrigids, living amidst leaf litter on the forest floor where they are well camouflaged. Their occurrence in Dominican amber suggests that resin was occasionally secreted directly onto the forest floor. This assumption is supported by the presence of other ground-dwelling orthopterans including Tridactylidae and Gryllotalpidae (HEADS in prep.). Such inclusions are however, very rare and in terms of numbers of specimens arboreal taxa would appear to dominate the orthopteran assemblage.

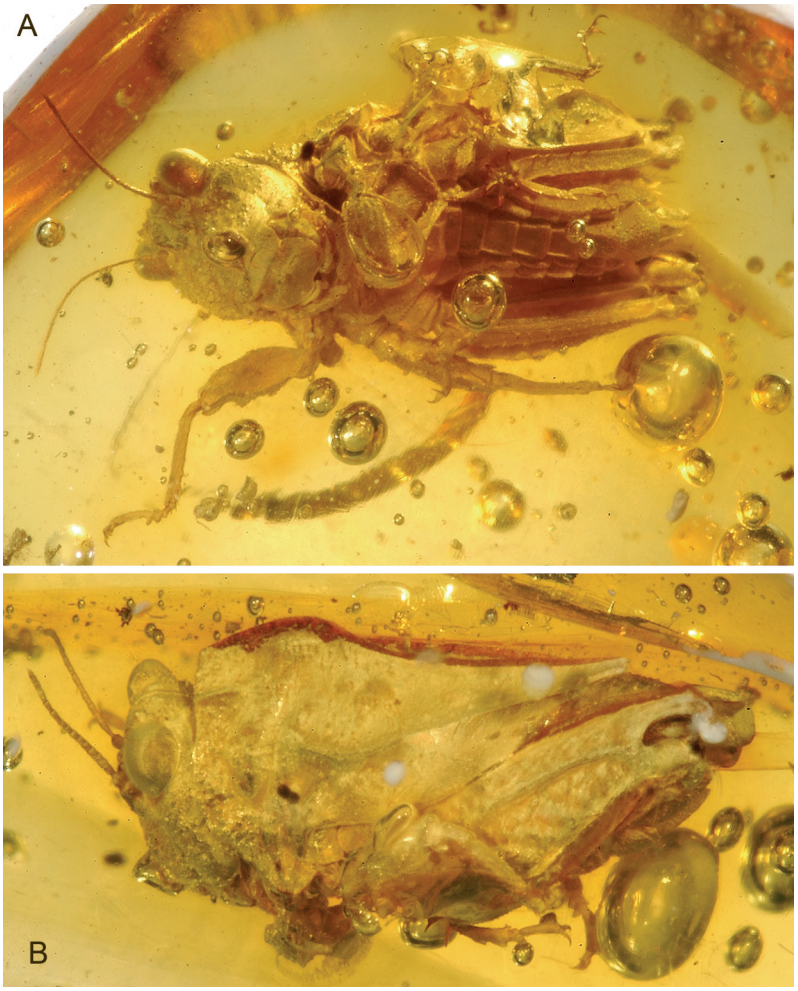


Fig. 7: Holotype of *Baeotettix lottiae* gen. et sp.nov. (AMNH DR-15-152); (**A**) oblique ventral view; and (**B**) dorso-lateral view of habitus. Dimensions are given in the text.

Given the complex and dynamic geological history of the West Indies, characterised by the emergence and submergence of landmasses and the establishment and subsequent disintegration of land bridges, understanding the evolution of the region's biota can be extraordinarily difficult (GRIMALDI & ENGEL 2005). The Miocene amber of the Dominican Republic offers unique insight into the evolution of the modern biota and the study of its inclusions are an essential component to our understanding of Caribbean natural history. The Dominican amber orthopteran fauna is distinctly tropical, dominated by trigonidiine and oecanthine gryllids and phaneropterine tettigoniids. Gryllotalpids, tetrigids and tridactylids are much rarer but provide important insight into the composition of the litter fauna of the Dominican amber forests.

Zusammenfassung

Aus miozänem Bernstein der Dominikanischen Republik werden zwei neue Zwergheuschrecken (Orthoptera: Tetrigidae: Cladonotinae) beschrieben. *Antillotettix ambarinus* sp.nov. und *Baeotettix lottiae* gen. et sp.nov. sind die ersten Tetrigiden, die in dominikanischem Bernstein nachgewiesen werden konnten. Zudem wird eine aktualisierte Liste der Tetrigidae von den Karibischen Inseln präsentiert.

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